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Huijing, P.A.J.B.M.

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MUSCULAR FORCE TRANSMISSION: A UNIFIED, DUAL OR MULTIPLE SYSTEM? A REVIEW AND SOME EXPLORATIVE EXPERIMENTAL RESULTS

P. A. Huijing

Instituut voor Fundamentele en Klinische Bewegingswetenschappen, Faculteit Bewegingswetenschappen, Vrije Universiteit, Amsterdam
Integrated Biomedical Engineering for Restoration of Human Function, Biomedisch Technologisch Instituut, Universiteit Twente, Enschede, The Netherlands

ABSTRACT

Structures contributing to force transmission in muscle are reviewed combining some historical and relatively recently published experimental data. Also, effects of aponeurotomy and tenotomy are reviewed shortly as well as some new experimental results regarding these interventions that reinforce the concept of myofascial force transmission. The review is also illustrated by some new images of single muscle fibres from Xenopus Laevis indicative of such transmission and some data about locations of insertion of human gluteus maximus muscle. From this review and the new material, emerges a line of thought indicating that mechanical connections between muscle fibres and intramuscular connective tissue play an important role in force transmission. New experimental observations are presented for non-spanning muscle (i.c., rat biceps femoris muscle), regarding the great variety of types of intramuscular connections that exist in addition to myo-tendinous junctions at the perimuscular ends of muscle fibres. Such connections are classified as (1) tapered end connections, (2) Myo-myonal junctions, (3) myo-epimysial junctions and (3) Myo-endomysial junctions. This line of thought is followed up by consideration of a possible role of connections of intra- and extramuscular connective tissue in force transmission out of the muscle. Experimental results of an explorative nature, regarding the interactions of extensor digitorum longus (EDL), tibialis anterior (TA) and hallucis longus (HAL) muscles within a relatively intact dorsal flexor compartment of the rat hind leg, indicate that: (1) length force properties of EDL are influenced by TA activity in a length dependent fashion. Depending on TA length, force exerted by EDL, kept at constant origin insertion distance, is variable and the effect is influenced by EDL length itself as well; (2) Force is transmitted from muscle to extramuscular connective tissue and vice versa. As a consequence force exerted at proximal and distal tendons of a muscle are not always equal. The difference being transmitted by extramuscular connective tissue and may appear at the tendons of other muscles or may be transmitted via connective tissue directly to bone. It is concluded that the system of force transmission from skeletal muscle should be considered as a multiple system.

KEYWORDS: Muscle, tendon, sarcolemma, connective tissue, endomysium, epimysium, perimysium, myotendinous junction, myofascial transmission, force transmission, non-spanning muscle fibres, myo-myonal junction, myo-endomysial junction, myo-epimysial junction, aponeurotomy.

INTRODUCTION

A condition sine qua non for controlled movement of the body of vertebrates is to exert muscular forces onto the bony skeleton to create a moment with respect to articular joints. In addition forces have to be exerted on the tissues of the joints to create mechanically stable conditions. The primary source of force for both purposes is the interaction of the contractile filaments within the intracellular milieu of muscle fibres. Therefore the force needs to be transmitted from the interior of muscle fibres through the cell membrane to structures attached to the skeleton. Regarding the number of

Address correspondence to: Prof. Peter A. Huijing Ph.D., Faculteit Bewegingswetenschappen, Vrije Universiteit, van de Boechorststr. 9 1081 BT Amsterdam. Fax: +31–20–444 8529. E-mail: P_A_J_B_M_Huijing@FBW.VU.NL.

recent publications we have to conclude that the subject of transmission of force is not very popular, either for physiologists or biomechanists. An explanation could simply be the idea that the mechanisms involved are relatively simple and well described and understood: For example in pennate muscle, force is transmitted from sarcomere to sarcomere arranged in series within the myofibrils. The myofibrils will directly and exclusively transmit force to a very specialised structure (the myotendinous junction), where the force is exerted onto the aponeuroses, which is continuous with the tendon that is attached to bone. Some reports consider it misleading to talk of 'attachment' of tendon to bone (Rogers, 1983). These authors consider one to be really continuous with the other, as collagen is the basis of both tissues, and bundles of collagen continue on from the tendon into the bone.

There is little doubt that force transmission will occur at the myotendinous junction and elegant experimental studies (e.g., Tidball & Daniel, 1986; Tidball, 1986; Tidball, 1991) as well as biomechanical modelling studies (e.g., Tidball, 1983) indicate that shearing of the basal lamina is the principal mechanism involved in transmission of force from the myofibril to the tendinous collagen. However, in contrast with the unified representation of in series force transmission, there are several recent and classical studies indicating that transmission of force from the muscle fibre is not limited to the myotendinous junction. The additional concept involves force transmission from the whole perimeter of muscle fibres. The fact that recently two keynote speakers at the Tokyo International Society of Biomechanics Congress (Huijing, 1999; Monti et al., 1999) dedicated most of their presentation to skeletal muscular force transmission may indicate a renewed interest in the complex features of this subject.

The principal aim of the present work is to review some relevant literature, both classical and recent, as well as present some explorative new experimental results and discuss their implications for force transmission from muscle.

CLASSICAL STUDIES REGARDING RELEVANT MORPHOLOGY: THE SARCOLEMMA AND ENDOMYSIUM

The study of microscopic aspects of non fixed muscular tissue commenced in the 17th century with the work of Antoni van Leeuwenhoek published in letters to Robert Hooke, secretary of the Royal Society of London (Leeuwenhoek, 1682). A description of the fibrilar character of muscle with some suggestion of striations and possibly myofibrils was the result.

In retrospect, a very important step ahead were the images of muscle fibres drawn by William Bowman (Bowman, 1840). He described single muscle fibres of the frog and snake (Fig. 1a), probably damaged in the process of dissection. The damage had caused an enormous contraction, which compromised the continuity of the myofibrils. Similar images were published also by Nagel (his Figs. 6–8) approximately one hundred years later (Nagel, 1935). A modern image of this type is shown in Figure 1, lower panel. This type of preparation revealed that a transparent tube, which at the time was referred to as the sarcolemma, surrounded the contents of the muscle fibre. Presently it is known that this structure is composed of the muscle cell membrane as well as the basal lamina and the endomysium.

In modern literature the term sarcolemma is more frequently reserved for the lipid bilayer which forms the cell membrane of the muscle fibre. However, it should be noted that also in a segment of modern literature, Bowman's nomenclature is still used (Street & Ramsey, 1965). Sometimes, it also may be found that the combination of basal lamina and endomysium is referred to as basal lamina (Carlson & Carlson, 1991).

To avoid such confusion of nomenclature, in the present work the muscle fibre's plasmalemma will be referred to as sarcolemma and the combination of the lipid bilayer cell membrane, the basal lamina and the endomysium is referred to as the sarcolemmal composite. It is this combined structure that is implicated in a crucial role in muscular force transmission.

FORCE EXERTED BY ISOLATED MUSCLE FIBRES AND ISOLATED FASCICLES

In the second part of the 20th century, a more general pioneering effort started the study isolated living cells. The 1952 experiments and model of propagation of the action potential in the giant axon of the squid by Hodgkin and Huxley (reprinted in 1990) and the experimental studies of (Buchtal, 1942) as well as Street and Ramsey (Ramsey & Street, 1940; Street & Ramsey, 1965) on muscle fibres are good examples.

During determination of length force characteristics, Ramsey and Street (Ramsey & Street, 1940; Street & Ramsey, 1965) confirmed for certain conditions the phenomenon of super-contraction, involving retraction of the myofibrils from a certain fraction of the muscle

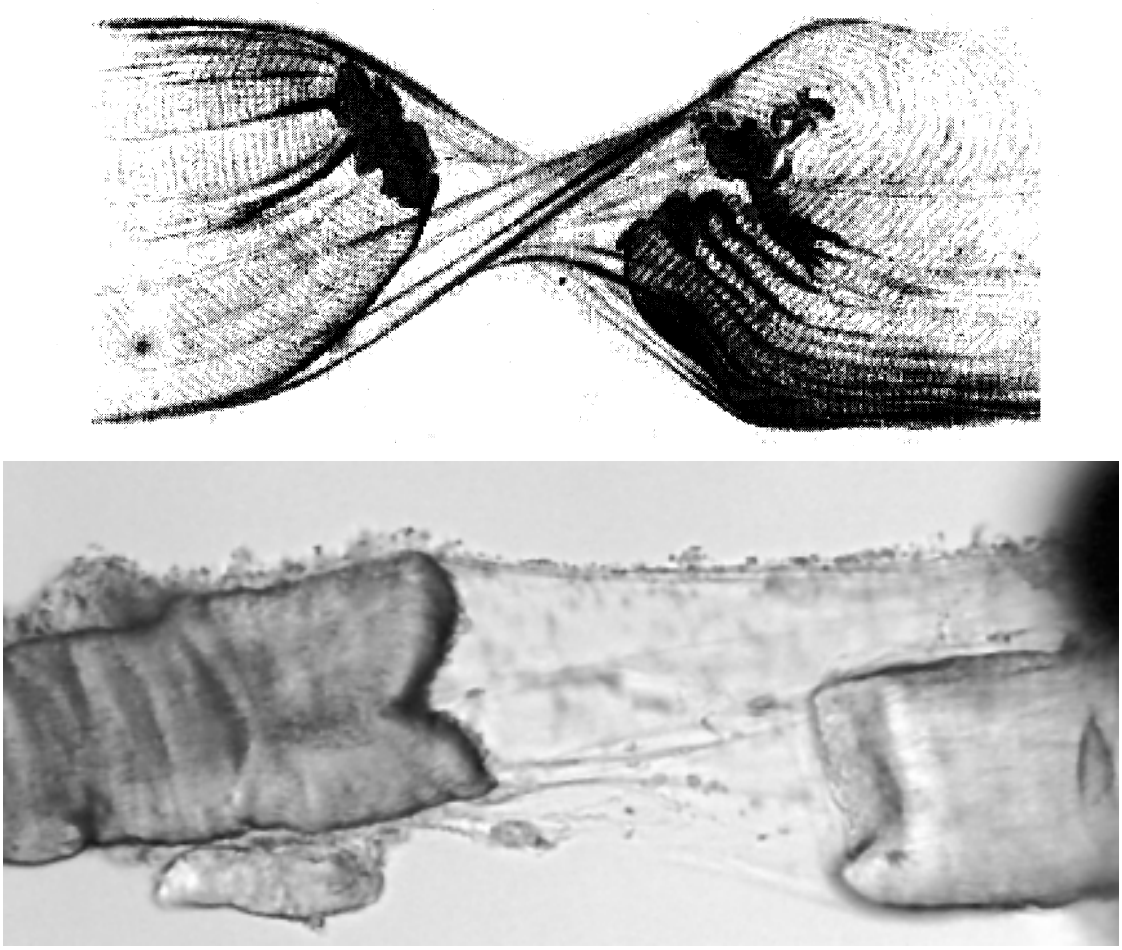

Fig. 1. Images showing the muscle fibre sarcolemmal composite.
Top panel: Reproduction of a drawing of Bowman (1840) showing a Boa constrictor muscle fibre in which striated materials have withdrawn in a segment of the fibre, leaving a view of what, at the time, was called the sarcolemma. Presently we know that this structure is composed of a cell membrane (plasmalemma) basal lamina and endomysium. In this article we refer to the structure as the sarcolemmal composite.
Bottom panel: Modern light micrograph of an isolated fibres of Xenopus iliofibularis muscle, in which damage to the plasma membrane has caused a supercontraction and tearing of the myofibrils across the full cross-section of the fibres. As a consequence the sarcolemmal composite is exposed.

fibre, seen by Bowman in the 19th century. An important and new observation was that, in the state of supercontraction, force was transmitted across the part of the muscle fibre without myofibrils. Evidently in series force transmission, in longitudinal direction towards the myotendinous junction, is not possible in this condition. Street and Ramsey (Street & Ramsey, 1965) concluded that the majority of force generated intracellularly was transmitted to the other half of the fibre via the sarcolemmal composite. The mechanical characteristics of the sarcolemma composite have been studied much later using similar preparations (Fields, 1970). Figure 2 shows some recent circumstantial evidence of a similar nature for lateral force transmission in isolated muscle fibres teased from Xenopus iliofibularis muscle. On contraction, the muscle fibre had torn its myotendinous junction. As passive force was subsequently exerted onto the fibre, at the end of the muscle fibre the tendinous material moved away from the muscle material as expected. However, despite the loss of connection at the myotendinous junction, the muscle fibre, with the exception of its damaged end could still be lengthened.

The original idea of Street and Ramsey, inspired Sibyl Street to perform experiments aimed exclusively at the study of force transmission in muscle fascicles. For that purpose single fibres within a small fascicle were partially isolated from the surrounding muscle fibres and connective tissue. The results (Street, 1983) were quite clear: (1) For the isolated single fibre segment located centrally along the length of the fascicle (i.e., at its centre) the continuity of the fascicle is maintained only the isolated muscle fibre. In such a

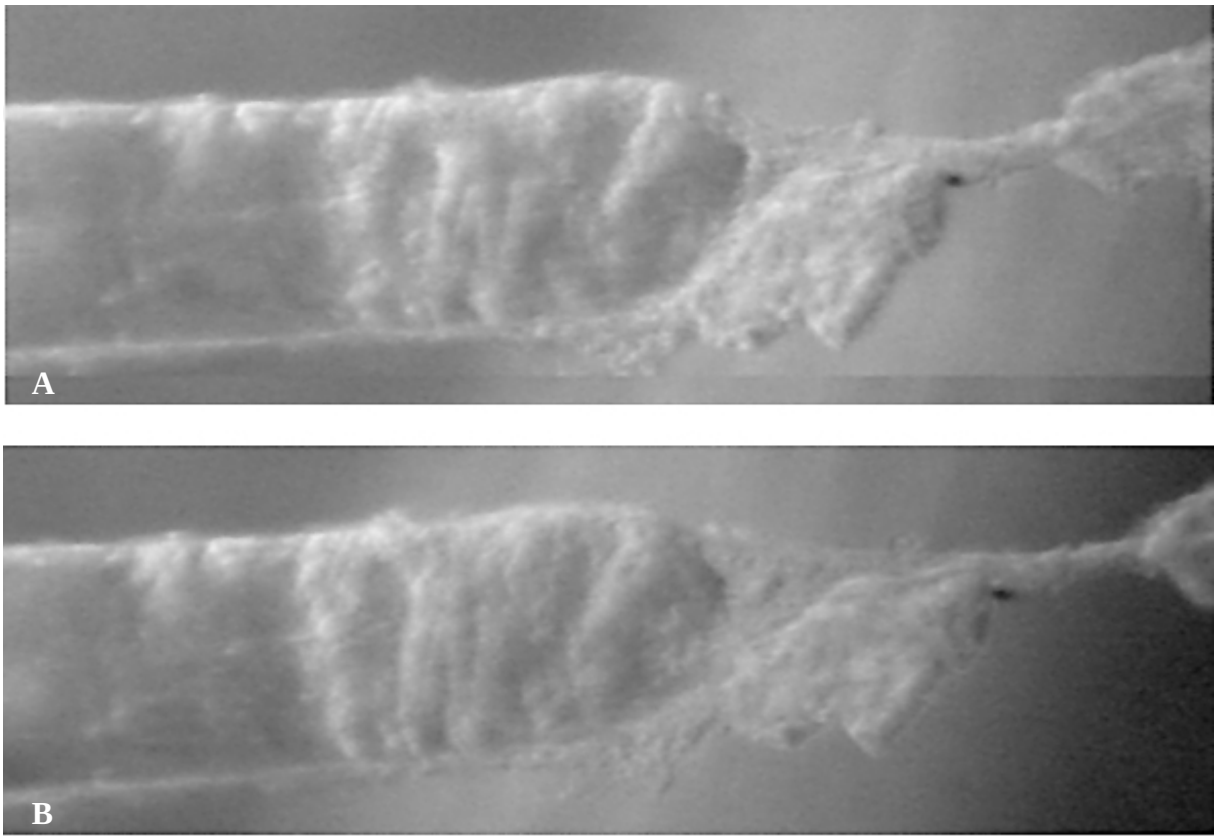

Fig. 2. Light micrographs showing the effects of stretch on a passive isolated muscle fibre with damaged myotendinous junction.
A. The isolated muscle fibre is shown at or just below its passive slack length, i.e., no passive force is exerted by the fibre on its environment. The area of the former myotendinous junction is shown just to the left of the centre of the image. At the myotendinous junction the contractile material has retracted a little (to the left side, conical shape), thus severing the myotendinous junction and exposing the sarcolemmal composite. The sarcolemmal composite itself is continuous with a thinner strand of tendinous tissue. Both are partly covered by a remaining glob of intramuscular connective tissue. At the right hand side a thicker part of the tendon is seen.
B. After the fibre has been stretched, most of the fibre has lengthened (as is evident also from the larger fibre segment in the field of view) and the tendinous material is stretched elastically. However, the retracted part of the contractile material close to the former myotendinous junction does not change its length. This is compatible with the fact that the myotendinous junction is not mechanically intact anymore, i.e., the myofibrils are not connected any more with the tendinous material. This is a fairly common damage in the process of isolating single fibres. The observation is that the major part of the muscle fibre can still be stretched by moving the fibre end at the right of the figure. This stretch can still take place despite the mechanical discontinuity at the former myotendinous junction. This indicates that the area of damage is bypassed mechanically by the sarcolemmal composite. This is an indication for myofascial transmission of force: The external force is transmitted via the endomysium onto those sarcomeres which are to the left of the retracted contractile material.

preparation, while passively stretching the whole fascicle, the non-isolated segment of a partially isolated passive muscle fibres was kept at similar sarcomere lengths as in surrounding muscle fibres. This similarity of sarcomere length was maintained by surrounding connective tissue and muscle fibres even on stretching of the fascicle. Any sarcomere length changes of the isolated muscle fibre were limited to those sarcomeres within the 'bare' part of the partially isolated fibre, until conditions became extreme and a redistribution of length changes occurred in the whole fibre; (2) A muscle fibre was partially isolated from the fascicle in such a way that its 'bare' part was located at the end of the fibre. Such an active partially isolated fibre exerted a similar force if the myotendinous end, not attached to the force transducer, was either loose or clamped to earth. In such conditions it is clear that sarcomeres, within the non-isolated part of such a muscle fibre, do not shorten to their active slack length (i.e., the length at which active force is generated but not exerted anymore on the environment) but are kept at much higher lengths. The force that keeps these sarcomeres at high lengths also allows transmission of force from the sarcomeres to the surrounding tissues. Street referred to such transmission as lateral force transmission. In electron microscopic images of shortened muscle fibres she noticed shapes that were consistent with connections from the Z-band to the sarcolemmal composite.

FORCE TRANSMISSION FROM MUSCLE FIBRES IN WHOLE MUSCLE

As indicated in the introduction, there is little doubt that force transmission will occur at the myotendinous junction (Tidball, 1983; Tidball, 1986; Tidball & Daniel, 1986; Tidball, 1991; Law & Tidball, 1993). However, it should be pointed out that experiments interfering with myotendious force transmission, as several discussed in the present work, are far easier to perform than experiments interfering with alternative locations of force transmission. Therefore, more than a decade ago, Woo and Buckwalter concluded (Woo & Buckwalter, 1987): "Although there is no direct, physiologic evidence to show that myotendinous junctions are sites of force transmission, their location at the end of muscle cells, where myofibrils are attached to the cell membrane supports this proposed function for these sites." To the best of our knowledge this situation has not changed since that time.

Alternative Locations of Muscle Fibre Attachment

It is important to note that a majority of muscles are not equipped with both a proper distal and proximal aponeurosis. In such cases one end of the muscle fibre may be attached to a number of structures:

a) Intramuscularly: non-spanning muscle fibres

Several muscles are composed of muscle fibres, which are attached to an aponeurosis only at one of their ends. Such fibres have been known for at least nearly a century (e.g., Huber, 1916; Lindhard, 1931). The other end of the muscle fibre is located somewhere in the middle of the muscle belly. Most authors refer to muscle containing these type of muscle fibres as in series-fibred muscle, because they believe the muscle fibres reaching in to the middle part of the muscle from either aponeurosis to be arranged in series. However, based on considerations of force transmission, recently the question has been raised again (Huijing, 1999) if such fibres really are all arranged in series or should rather be considered as parallel arranged muscle fibres. For that reason we use the more neutral name of non-spanning muscle fibres in the present work, as such fibres do not span the distance between two aponeuroses within a muscle. Non-spanning fibres may overlap each other for more than 40% of their length. The lengths of their overlapping portions generally corresponded to the length of the tapering segments (Hijikata et al., 1993). In any case, for non-spanning tapering designs of muscle it is clear that the force must be transmitted also in another way than by myotendinous transmission (e.g., Hijikata, 1992; Trotter & Purslow, 1992; Hijikata, 1993; Trotter, 1993; Purslow & Trotter, 1994; Trotter et al., 1995; Hijikata et al., 1999).

Rat biceps femoris muscle is an example of a muscle consisting of non-spanning muscle fibres as well as spanning fibres. After fixation and treatment with potassium hydroxide (5.6% for 30 min), preparations of single fibres or a small number of related muscle fibres from this muscle were prepared. Figures 3 and 4 show fibre ends encountered in these preparations.

In general, at intramuscular locations, four types of morphologies of fibre ends of non-spanning muscle fibres are reported:

Tapered end fibres. Most non-spanning muscle fibres have tapered ends. No specialised microscopic junctional structures are present, as force is thought to be transmitted via the full periphery of the tapering ends of the muscle fibres. The basic idea proposed by a group of authors (e.g., Trotter & Purslow, 1992; Trotter, 1993; Purslow & Trotter, 1994; Trotter et al., 1995) was that force is transmitted from muscle fibre to adjacent muscle fibres by shearing of the sarcolemmal composites. Force of non-spanning muscle fibres could then be transmitted to the tendons by myotendinous junctions of adjacent muscle fibres, which could either be non-spanning or spanning the distance between proximal and distal aponeuroses. Some rat biceps femoris non-spanning fibres show tapering ends and should be classified in this category (e.g., Figs. 3B and C).

Myo-myonal junctions. Far more rarely (according to, e.g., Trotter, 1990) non-tapering fibre ends are reported for nonspanning muscle fibres ending within the muscle belly. Such fibre ends show a similarity to those of myo-tendinous junctions and may be partial or entail the full diameter of the muscle fibre. They are referred to as myo-myous (Trotter, 1990), myo-myonal (Hijikata et al., 1993; Zenker et al., 1990; Snobl et al., 1998) or myomuscular junctions (Hijikata et al., 1999) They were first reported within eye muscles several decades ago (for references see Zenker et al., 1990). Torigoe (1987) proposed the following classification: (a) junctions in which all interfibre contacts were firm, without any connective tissue, and deeply invaginated; (b) junctions in which numerous collagen fibres were visible in the space between the two separate opposing muscle fibres; (c) an intermediate type between (a) and (b), i.e., a junction with partial contacts. Figure 3D shows an example of a fibre that seems to be tapering, but yet shows structures that seems to meet criteria (2a)

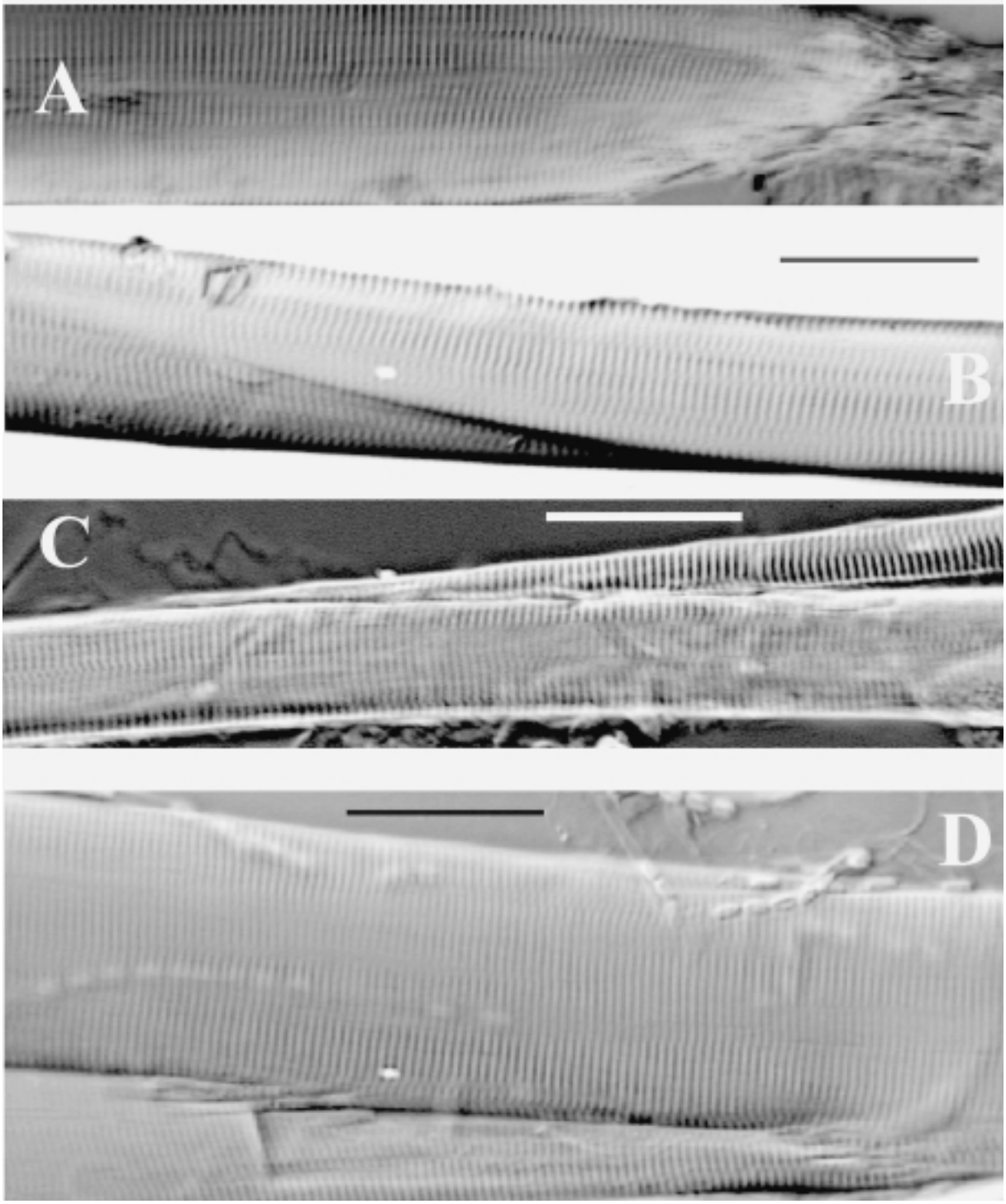

Fig. 3. Light micrographs showing different types of fibre ends encountered in rat biceps femoris muscle (I).
A. Myotendinous junction by which a muscle fibre is attached to the aponeurosis. Note the tendinous material at the right of the image.
B. & C. Examples of muscle fibres tapering to a thin end in the middle of the muscle belly. The tapering ends are thought to connect to the endomysium.
D. A tapering muscle fibre end in the middle of the muscle belly showing multiple connections resembling the myotendinous junction in shape. These connections could be either myo-myonal connections or myofasacial connections (see text). The diskoid shapes are red blood cells in a capillary.
Bars indicate a distance of 50 μm. To enhance viewing of connective tissue structures the images are presented in negative view.

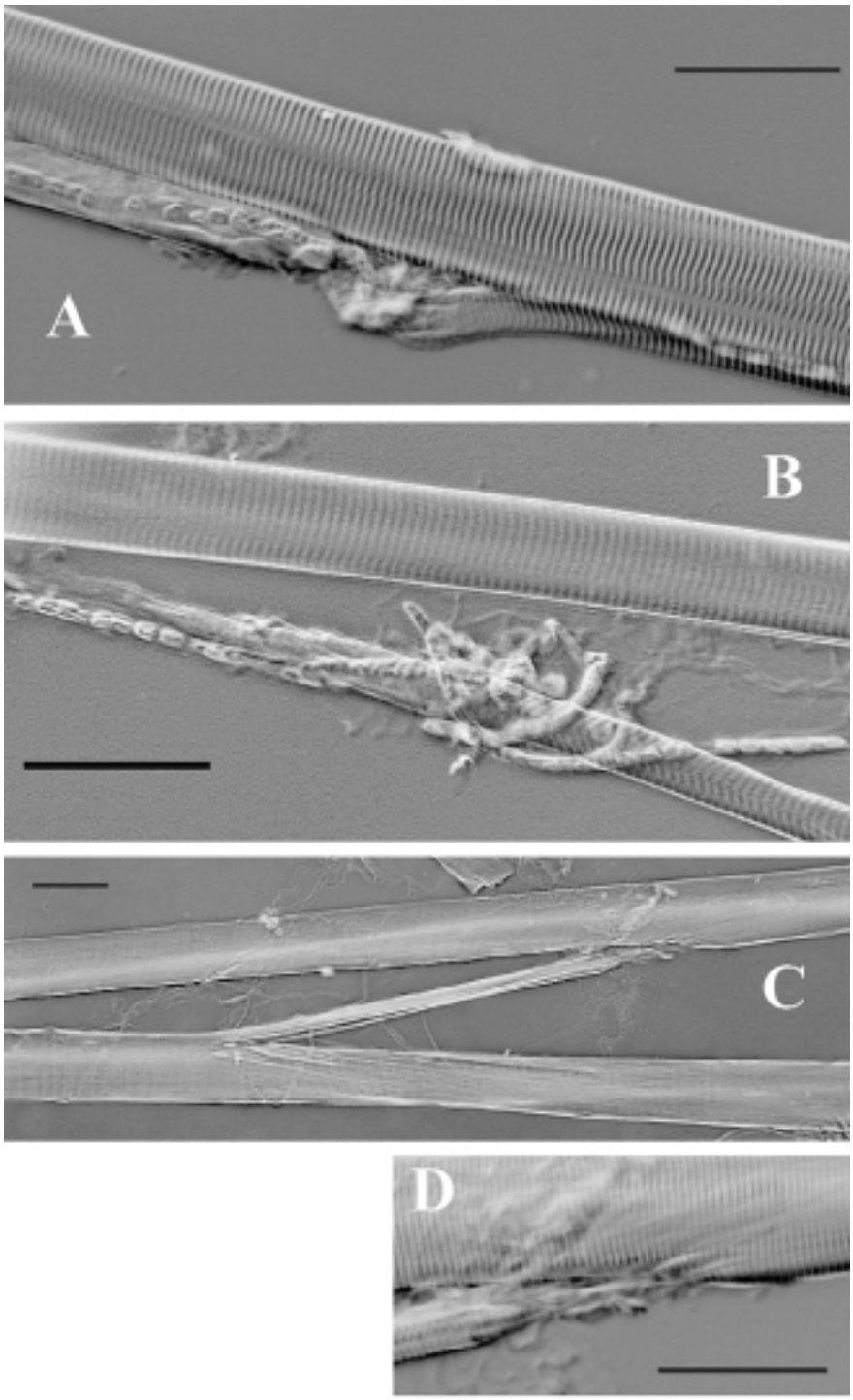

Fig. 4. Light micrographs showing different types of fibre ends encountered in rat biceps femoris muscle (II).
A. A structure, resembling that of a myotendinous junction, that is connected to connective tissue (presumably endo- or perimysium) in the middle of the muscle belly. This is classified as a myo-endomysial junction (see text).
B. A thin muscle fibre that tapers to an extremely thin end (in the left part of the image), but seems to be connected at that end with a myo-endomysial connection to the connective tissue apparatus of the muscle.
C. Two adjacent muscle fibres which have been moved apart some distance in the process of preparation to show a connection of part of the bottom fibre to structures that are related with the top fibre.
D. A higher magnified view of image C in the area of proximity of the thin strand of the lower muscle fibre with the adjacent fibre. Note that the strand of muscle fibre is connected to endomysial tissue as is also evident from the strain seen in structures below the larger fibre.
The diskoid shapes in (A) and (B) are red blood cells in a capillary. Bars indicate a distance of 50 μm. To enhance viewing of connective tissue structures the images are presented in negative view.

or (2c). Note the partial connections of this fibre to its neighbour at two proximate locations.

A major feature of type (2a) junctions is that the two linked muscle fibres may share aspects of one basal lamina (Hijikata & Ishikawa, 1997; Hijikata et al., 1993). At some locations within one such junction a shared lamina densa is seen, and the junctional processes adhere so closely to each other that no collagen fibrils could penetrate into their invaginations (Torigoe & Nakamura, 1987). At other locations within the same junction, each muscle fibre may have their own lamina densa. Between such two dense laminas, filamentous material is found (Hijikata et al., 1992). Presently, the question about the mechanical type of arrangement of muscle fibres by myo-myonal junctions can not be answered unequivocally but in this case a in series arrangement seems to be most likely.

Myo-epimysial junctions. Only one article was encountered by us (Järvinen et al., 1992), reporting on this type of myo-fascial junction. This type was found in rat soleus and gastrocnemius muscles. It has a morphology resembling that of the myotendinous junction, involving typical invaginations of the sarcolemma and basal lamina. However it was found at the lateral surface area of a muscle fibre. A major distinction with myotendinous junctions is that these junctions are directed at right angles with respect to the longitudinal direction of the muscle fibre. The depth of their invaginations (0.5–2 μm) was less than myotendinous junctional invaginations. It should be noted that this type of junction was found only in superficial muscle fibres at the interface between muscle and the epimysium.

Myo-endomysial junctions. Figure 4 shows examples of another type of junctions found in rat biceps femoris muscle. Also here the characteristic invaginated structure may be recognised, approximately in longitudinal direction of the muscle fibre. Note, however, that in several preparations shown the junctional invaginations are not filled with processes from attaching muscle fibres but seem to be filled by endomysial connective tissue. Therefore such junctions should most adequately be classified as myo-endomysial junctions.

It is clear that a wide variety of mechanical connections could be operational for nonspanning muscle fibres. The mechanical nature of the connections to either intramuscular connective tissue or other muscle fibres needs further detailed attention. Only for some myo-myous junctions without intervening endomysium, it seems most probable that muscle fibres involved are arranged in series. If any endomysium is involved in the connection, one seriously has to consider the possibility that force will be transmitted to the endomysium rather than neighbouring muscle fibres, which would implicate a parallel rather than an in series connection of muscle fibres. If this parallel arrangement is true, the non-spanning fibred muscle could be considered functionally as a type of pennate muscle in which for a given volume of muscle the physiological cross section is enlarged at the expense of number of sarcomeres in series (fibre length).

b) Extramuscular locations of attachment

Rather than attaching to a perimuscular or intramuscular aponeurosis, muscle fibres may end on several other structures at the muscle's periphery:

Cortical bone. A prominent feature of bone is its ability to support moments (e.g., Otten, 1988) as well as compressive forces accompanying muscle contraction (Teng & Herring, 1998), in contrast to aponeuroses which have rather low stiffness against bending and thus rotation. Bony attachments of muscle fibres are supposed to resemble the attachment of tendon to bone, it is not fully clear if such a structure has mechanical properties similar to those of myotendinous junctions at intramuscular aponeuroses or other fascia. However, there is some evidence available that mechanical differences between aponeuroses and bony attachments do affect muscular properties substantially (Willems & Huijing, 1994a, 1994b; Huijing, 1996).

Periosteum. Not all muscle fibres having their fibre ends near bone connect to the bone itself. For example in multipennate rat medial pterygoid muscle, muscle fibres span distances between proximal and distal aponeuroses and between aponeuroses and the periosteum (Matsumoto & Katsura, 1987). The periosteum itself is connected tightly to the cortical bone by special collagen fibres, which are referred to as Sharpey fibres. Therefore, this connective tissue component surrounding the bone also is an adequate insertion area for muscle fibres. There is evidence that adaptation of the periosteum to muscle and tendon attachment may affect mechanical properties of periosteum are strongly influenced by the ligament and muscle attachments (Uchiyama et al., 1988).

Extramuscular fascia. Human m. gluteus maximus is a very good example. It has been well known for quite some time that it has a rather complex insertion (e.g., Benninghoff, 1938). Recent work from our laboratory shows that a minimum of 75% of the muscle fibres do insert on the tractus iliotibialis (i.e., the reinforced general fascia (fascia lata) surrounding the thigh. Only a maximum of 25% of the fibres do insert

on locations on the femur (i.e., either on bone or periosteum). These observations are based on dissecting the muscle parts according to the location insertion and determining their relative mass (unpublished observations, Schutte & Huijing). For some individuals even 100% of the fibres attach to tractus iliotibialis locations as a sole insertion for this very sizeable muscle. As the fascia lata itself inserts also on the tibia, it is conceivable that the gluteus maximus muscle should be considered a biarticular muscle. A possibility for mechanical interaction gluteus maximus muscle with spinal muscles via the thoracolumbar fascia has also been described recently (Vleeming et al., 1995). This general fascia can be considered as a connective tissue tunnel of sizeable diameter subdivided by the intermuscular septa into muscle group compartments. A similar total lack of bone or bone related origins of human soleus muscle was also reported for certain individuals (Ekenman et al., 1995).

It should also be realised that in several muscles, the aponeuroses may be an integral part of the intermuscular septa. An example in case could be the relationship between the anterior septum of the lower human leg acting as the aponeurosis for both the extensor hallucis longus muscle and peroneus longus muscles. A comparable situation was described for several muscles of the forearm region of the rat (Wal, 1988). In some reports (e.g., Sakamoto, 1996), the intra- or perimuscular aponeurosis is regarded as a specialisation of the perimysial sheaths or part of the epimysium. It is clear that such relationships need further detailed morphological and histological study to determine the best way of classifying these structures. An important task will be to identify the interactions of these structures with other elements of the extracellular matrix.

INTRAMUSCULAR FORCE TRANSMISSION WITHIN ISOLATED MUSCLE: THE MYOFASCIAL ROUTE

The anatomy of rat extensor digitorum longus muscle (EDL), being extraordinary, was described in some detail a decade ago (Balice-Gordon & Thompson, 1988). The muscle is composed of spanning muscle fibres. The proximal part of the muscle must without doubt be considered a one-unit muscle: There the muscle has one aponeurosis to which all its muscle fibres attach under a modest angle of pennation. In contrast, distally the question could be raised if there is one muscle or four: the muscle is equipped with four separate aponeuroses, which define four segments of the EDL muscle fibres population. Each of these aponeuroses is attached to a long tendon, which insert on the terminal digits of either toe II, II, IV and V. This particularly structure makes EDL an attractive object to study force transmission.

a) Acute effects of tenotomy

Tenotomy of distal tendons of EDL effectively divides the population of EDL muscle fibres into two compartments: (1) A group of fibres with normal myotendinous function at both ends and (2) a group of muscle fibres, which are at their proximal end still attached to their aponeuroses, but no longer have connections to the muscle's insertion via that aponeurosis.

As a consequence of tenotomy, normal myotendinous functions of fibres of the second group will be interfered with at last at the proximal fibre end. Progressive tenotomy of distal tendons II, III and IV close to the end of the distal aponeuroses (Huijing et al., 1998) progressively prevents distal myotendinous transmission of force for 23 to 45% of the muscular physiological cross sectional area. For fully recruited maximally activated but tenotomised EDL, muscle optimum force exerted on the proximal tendon decreased only by maximally 16%.

Much as in Street's (1983) results, the active fibres without the capability of distal myotendinous force transmission remained at high lengths determined by muscle tendon complex length. The explanation provided for this phenomenon is myofascial force transmission (Huijing et al., 1998; Huijing, 1999). The force generated within muscle fibres is transmitted onto the intramuscular connective tissue system, consisting of endomysium, perimysium and epimysium elements. The transmission is proposed to be brought about by shearing of the basal lamina of the muscle fibres (Huijing, 1999) and force is transmitted onto the endomysium. The endo-perimysial system of connective tissue is continuous throughout the muscle belly of EDL and thus capable of transmitting force to the segment of this system within head V, in which myotendinous function remained unaffected. There the connective tissue is connected via the distal aponeurosis of this head to the tendon and the skeleton. In such a situation it must be concluded that the endomysial-perimysial-epimysial connective tissue system is part of the series elastic element.

b) Acute effects of intramuscular fasciatomy

Further evidence for such a theory of force transmission is obtained from experiments, in which the connective

tissue interface between EDL segments IV and V is damaged along the direction of the muscle fibres for a certain length. These interventions were performed following tenotomy II through IV, (Huijing et al., 1998; Huijing, 1999). Originally this intervention was referred to as myotomy (Huijing et al., 1998), however, a better name seems to be intramuscular fasciatomy, since the connective tissue (intramuscular fascial system) is damaged rather than the muscle tissue per se.

Intramuscular fasciatomy resulted in a decrease of intramuscular force transmission dependent on the length of the interface that was destroyed (Huijing et al., 1998). Less force was produced because proximal fibres, having normal myotendinous functions only at their proximal end, shortened more than after tenotomy. It should be noted, however, that even after damaging the EDL interface between muscle segment IV and V for up to approximately two thirds along the length of the muscle fibres myofascial force transmission was not fully obliterated. This was evident from a remaining muscle length dependence of proximal fibre length and elevated levels of force compared to values of physiological cross-sectional area of fibres with normal myotendinous functions at both ends.

c) Acute effects of intramuscular aponeurotomy

This intervention is applied clinically, to lengthen overly short spastic muscles (e.g., Thom & Asperger, 1982; Baumann & Koch, 1989; Brunner, 1998). In contrast to the studies discussed below it was applied as a tool to probe fundamental muscular properties. Proximal intramuscular aponeurotomy per se has an effect similar to that of tenotomy: It effectively divides the population of muscle fibres from a muscle into two compartments: (1) A group of fibres with normal myotendinous function at both ends and (2) a group of muscle fibres, which are at their proximal end still attached to their part of the aponeurosis, but no longer have connections to the muscle's origin or insertion via that aponeurosis. However, a secondary effect is seen as soon as the muscle is brought to higher length and is activated: The muscle's connective tissue apparatus tears for some distance along the direction of the muscle fibres below the location of the aponeurotomy. This spontaneous tearing resembles the intramuscular fasciatomy brought about purposefully by experimenters in some studies (Huijing et al., 1998).

Following proximal intramuscular aponeurotomy in rat medial gastrocnemius muscle (GM), the distal part of the proximal aponeurosis is not directly connected anymore to the muscles origin. Despite the aponeurotomy and its concomitant destruction of the intramuscular connective tissue system below the location of the aponeurotomy, the muscle fibres attached proximally to the part of the proximal aponeurosis, which is 'freed' from the muscle origin, still attain higher lengths as the muscle is brought to higher muscle lengths (Jaspers et al., 1999). This is considered as a crucial proof of myofascial force transmission. However it should be noted that, unlike effects of tenotomy, but similar to effects of intramuscular fasciatomy, the effects on muscle force are very limited. It has been concluded that after tearing of the connective tissue myofascial force transmission still takes place, but that its beneficial effects on muscle force are almost fully balanced by local effects on sarcomere lengths elsewhere in the muscle leading to a decrease of force (Jaspers et al., 1999).

Finite element modelling of the intervention allowing a detailed analysis of (EDL) muscle morphology that can never be equalled experimentally supports this conclusion (Linden, 1998). For example, at muscle optimum lengths, very high strains in the direction of the active muscle fibres are seen locally in the part with of the muscle with normal myotendinous functions, which was previously thought of as the 'unaffected' part of the muscle. Maximal local strain in this part of the active muscle before aponeurotomy are limited to the range of approximately –4 and +4%, whereas after aponeurotomy and its full morphological consequences a range of –30 to +30% due to very high local active stress in muscle fibres (Fig. 5) is found (Linden, 1998).

A very interesting feature is encountered as experimental intramuscular aponeurotomy is performed on the proximal aponeurosis of EDL muscle at the location of the interface between head IV and IV. This distinguishes groups of fibres with normal myotendinous function (head II through IV) from fibres without normal myotendinous functions (head V) respectively. Note with such a location of intervention quite comparable muscle compartments are used as those after distal tenotomy (II through IV) but with inverted relationships regarding normal and abnormal myotendinous functions (Fig. 6).

In contrasts to the distal tenotomy experiment, proximal aponeurotomy of isolated EDL causes subsequential rupture of the muscle connective tissue below the location of the aponeurotomy with severe consequences for myofascial force transmission, much as it did after proximal aponeurotomy in GM. A detailed analysis of these comparisons is being made presently (Jaspers, Brunner, Baan & Huijing, unpublished observations).

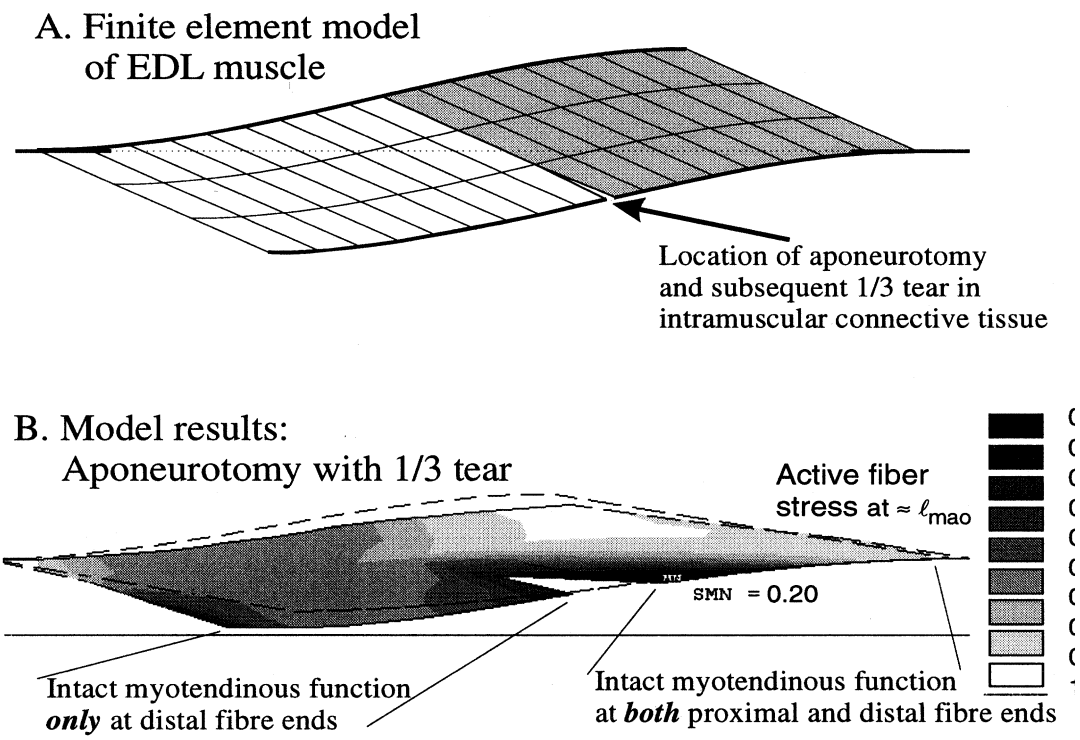

Fig. 5. Finite element modelling of muscle (Linden, 1998). The effects of aponeurotomy in a modeled muscle with a geometry resembling that of the rat extensor digitorum longus muscle (EDL).
The geometry of EDL at muscle optimum length in the passive and active state active is shown in outline. Shading indicates active fibre stress in the direction of the muscle fibers. An assumed continuous distal aponeurosis has been cut in its middle, and the model muscle allowed to tear along the direction of the muscle fibres for approximately 1/3 of their length. Two parts of the muscle are distinguished: (1) a distal part of which the fibres have intact myo-tendinous functions only at one end, since the aponeurosis to which these fibers are attached distally is no longer connected directly to the origin.
And (2) a proximal part in which the muscle fibres have normal myo-tendious function at both ends. Note the high differences in local stress.

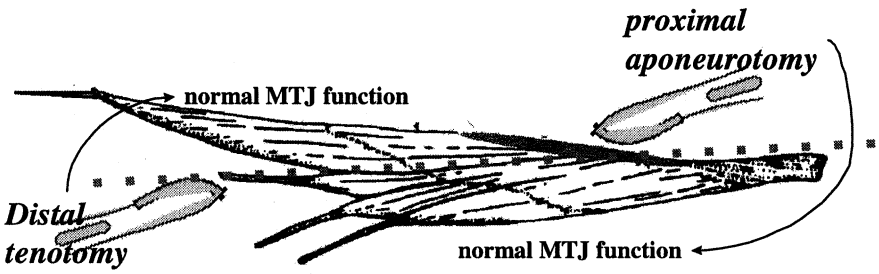

Fig. 6. Schematic representation of rat EDL muscle showing that proximal aponeurotomy and distal tenotomy-(IV) divides the muscle in comparable compartments, but with opposite consequences for these compartments regarding the segment with normal myo-tendinous functions at both distal and proximal fibre ends. The line of filled squares indicates the border between the two compartments.

THE (SUPRA) MOLECULAR ORGANISATION OF MYOFASCIAL FORCE TRANSMISSION

For a detailed description of the molecular structures that could transmit force from the intracellular myofibril associated milieu through the lipid cell membrane to the basal lamina and endomysium we refer the reader to recent reviews (Berthier & Blaineau, 1997; Patel & Lieber, 1997). Berthier and Blaineau distinguish two domains that could be important for force transmission: (1) The myotendinous junction and (2) the costamere domain. The costamere domain can be described as follows (Pardo et al., 1983): Perpendicular to the longitudinal axis of the muscle fibre, bands of specialised

molecules encircle the muscle cell and repeat along its length with a periodicity corresponding to the subjacent sarcomeres. Because of their appearance and probable function, the transverse elements of the lattice are called costameres (Latin costa, rib; Greek meros, part) (Pardo et al., 1983).

It should be noted that these domains distinguished are not fully exclusive as costameres are found also within the lateral aspects of the myotendinous junction. Therefore an improved classification would probably be: (a) a terminal domain of the myotendinous junction, at which α actin filaments of the final half sarcomeres insert on the sarcolemma associated molecules; and (b) a costamere domain at full lateral aspects of the muscle fibre (including those of the invaginations of the myotendinous junction), Berthier and Blaineau (1997) distinguish the costamere domain in three parallel segments of the sarcoplastmatic cytoskeleton that could potentially play a role in (myofascial) force transmission. It should be noted however that, despite a fairly detailed description of candidate molecules it is clear that the molecular nature of the complete link form the saromeric cytoskeleton to the basal lamina is not clear. Such elements of missing links is also apparent implicitly within the review of (Patel & Lieber, 1997).

The other necessary connection for force transmission from the basal lamina to the endomysium may be regarded as a missing link also. Judging from the elegant images of Nishimura et al. (1996) proteoglycans could be implicated in this connection. Proteoglycans consist of a core protein to which glycosaminoglycan chains and various oxygen and nitrogen linked oligosaccharide chains are attached covalently. Cytochemical identification of proteoglycans (Nishimura et al., 1996) make it clear that at the interface of basal lamina and endomysium heparan sulphate proteoglycans play some role.

In any case, the experimental results on EDL force transmission, presented above, make it likely that molecular links from the sarcomeric cytoskeleton via sarcolemma associated systems to the basal lamina and endomysium are present that are capable of transmitting substantial parts of muscle force.

INTEGRATION OF MYOTENDINOUS AND MYOFASCIAL FORCE TRANSMISSION?

The experimental results described above for rat EDL or GM muscle were obtained with these muscles isolated from surrounding connective tissue, but not from normal circulation and innervation. After aponeurotomy or tenotomy, such experimental conditions dictate that force must be transmitted eventually to a tendon. This must be true even if the force is transmitted towards that structure by myofascial pathways. In principle there are two potential paths available: (1) force could be transmitted onto intracellular structures of active muscle fibres with normal myotendinous junctions and from there onto the tendon via these junctions. In such a case the muscle fibres bearing the additional force are expected to be brought to higher lengths to reach a new mechanical equilibrium. In contrast to such expectations no net length changes were reported for fibres with intact myotendinous functions after tenotomy and aponeurotomy (Fig. 7). Therefore use of the second path seems more likely.

(2) The force is transmitted solely to the endomysium and thus stays outside the muscle fibres. In such a case the endomysium acts as a scaffold to which muscle fibres may form mechanical connections. Such mechanical connections could be covalent bonds. However, hydrogen bonds, electrostatic interaction and van der Waals forces could in principle also be involved.

Force transmission from the endomysium to the tendon is possible because, under physiological conditions, the network of intramuscular tunnels of connective tissue (endomysium-perimysium-epimysium) is connected to the aponeurosis (e.g., Scott & Loeb, 1995), which in turn is continuous with a tendon. Therefore, its seems likely that, in isolated muscle, myofascially and myotendinously transmitted forces are re-integrated at the aponeurosis. If such integration is always the case exclusively, it may be reasonable to consider the system of force transmission as a unified system with subdivisions.

However in such considerations the following has to be weighed as well: In isolated muscle, myofascial and myotendinous transmission to the aponeurosis form the *exclusive* paths only because *any* potential for alternative force transmission has been removed by dissection of the muscle from its surrounding tissues. In that respect, the widely accepted use of the term *in situ* seems inappropriate for such experiments involving dissected muscles.

MYOFASCIAL FORCE TRANSMISSION AS A POTENTIAL *EXTRA*-MUSCULAR PATH FOR TRANSMITTING MUSCLE FORCE

In vivo, and in experimental circumstances in which the potential connections between the connective tissue of

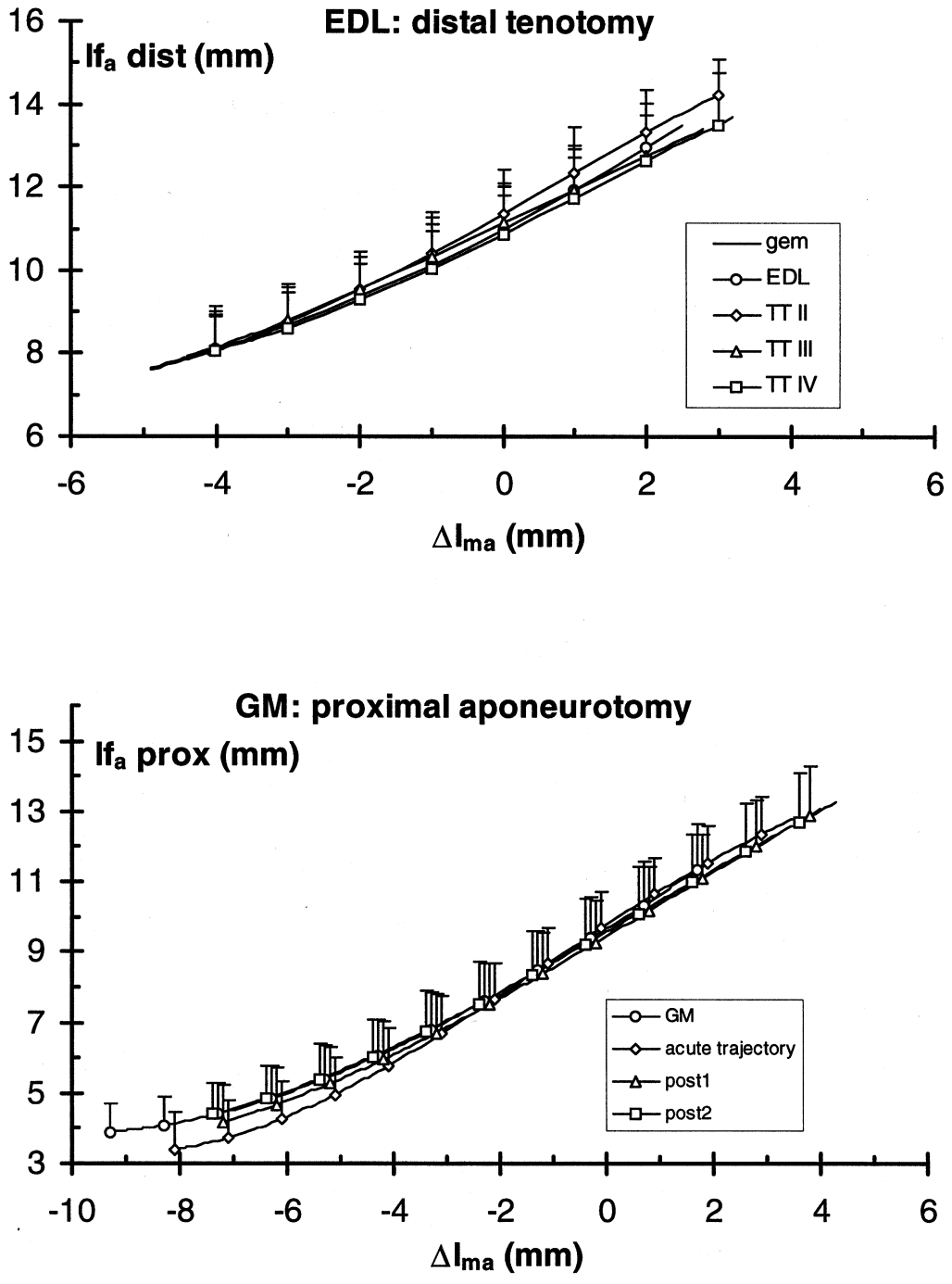

Fig. 7. The relationship between muscle length and length of fibres, which have intact myotendinous function at both proximal and distal ends, before and after tenotomy and aponeurotomy of the muscle of which they are a part.
A. For distal fibers within head V of rat extensor digitorum longus muscle before and after cumulative distal tenotomy (EDL tendon II through IV). The length of active distal fibres is denoted as lf_a dist.
B. For proximal fibers of rat gastrocnemius medialis muscle before and after proximal aponeurotomy. The length of active proximal fibres is denoted as lf_a prox.
Means and standard deviation are shown. Muscle length is expressed as deviation (Δl_{ma}) its optimum length, i.e., the length at which active force is optimal. Note that in neither experiment significant changes of fibre length could be shown despite the fact that force from approximately half of the physiological cross-section of the muscle is exerted onto the muscle part with intact myo-tendinous functions at both fibre ends. If force would be transmitted from muscle fibre onto muscle fibre significant length changes would be expected. Therefore it is likely that force is transmitted onto the endomysium and perimysium and from there to the aponeuroses.

the muscle and the surrounding tissues have not been obliterated, it is conceivable that force leaves the muscle as it is transmitted through the connective tissue system of the whole limb by other ways than a tendon, as has been proposed recently (Huijing, 1999).

The concept of potential extramuscular force transmission has been inspired by the results of intramuscular force transmission discussed above for EDL tenotomy experiments, plus the realisation that so called 'loose connective tissue' that is rather compliant and weak under tensile stress, may be considerable stiffer and stronger under shear stress (Huijing et al., 1998). It should be noted however that the mechanical characteristics of connections between intra- and extramuscular connective tissue components under different types of loading are not known. Therefore there is no unequivocal evidence regarding the feasibility of extramuscular myofascial force transmission as yet.

However a limited amount of evidence of a circumstantial nature that is in accordance with such a phenomenon can be found in the literature (Gregor et al., 1988; Riewald & Delp, 1996). Such evidence has been reviewed recently (Huijing, 1999) and will only be summarised here. The evidence concerns:

(1) Unexpected high forces on the Achilles tendon during gait of the cat, in which the triceps surae muscles are definitely active only submaximally. A comparison of this force to the Achilles' tendon force, of the same animal during maximal isometric contraction in an isolated muscle experiment *in situ*, shows that the force measured during gait is higher despite differences of level of activation and effects of velocity of shortening (Gregor et al., 1988). If this phenomenon is explained by myofascial force transmission, it would be an example of *extramuscular*-muscular force transmission through the connective tissue network of the limb.

(2) Unexpected exertion of knee extension moments on intramuscular stimulation of rectus femoris muscle in patients after transplantation of the distal tendon of this muscle to flexor locations at the knee.

Riewald and Delp (1996) hypothesised that in some way rectus femoris muscle force was transmitted to knee extensor muscles. An alternative explanation should be considered as well. As the operation involved interference with the connective tissue system of the upper leg exclusively at its distal end, myofascial force transmission could take place at the proximal end of the muscle. Such transmission could have an extending effect at the knee in two ways: (a) By transmission of the force to other aponeuroses within the quadriceps muscle, and from there to the patellar tendon (intra- or intermuscular transmission, depending on the view of the quadriceps muscle as one or more muscles); or (b) Through extra- muscular paths, (such as, for example, the intermuscular septum) to connective tissue elements crossing the knee joint on the extensor side of its axis. In the latter case the term intra- or intermuscular transmission would not be adequate. Therefore we will refer to such transmission as extramuscular myofascial force transmission.

It is not clear from Riewald and Delp's work, if any myofascial force transmission was still feasible at the distal, transplanted end of the rectus femoris muscle. However it should be noted that, even if force transmission in this distal part of the muscle were limited to myotendinous force transmission, a knee flexion moment would be exerted by this part of the muscle, due to its transplantation to the flexor side of the joint. This is in contrast with the presumed myofascial force transmission of the proximal part yielding an extensor moment at the knee. If this is indeed what occurred, the muscle has become its own antagonist.

INTERMUSCULAR INTERACTION AND EXTRAMUSCULAR MYOFASCIAL FORE TRANSMISSION: SOME EXPLORATIVE EXPERIMENTAL RESULTS

Extramuscular myofascial force transmission would be expected to cause interaction between the properties of, at least, adjacent muscles since the concept supposes mechanical connections of some stiffness between adjacent morphological structures. If no interaction would be found such force transmission would be rather unlikely. The intermuscular interaction could appear in many forms. An example would be, holding one muscle at different lengths would affect properties of the adjacent muscle. Such potential interactions of rat EDL and tibialis anterior (TA) muscles were studied in explorative experiments.

A Short Summary of Methods

a) Interaction of TA length change with EDL proximal force

At the lower leg and a part of the upper leg skin was removed and the general fascia was opened to expose the biceps femoris muscle. The insertion of the biceps femoris muscle was cut and a major part of the muscle removed to expose the sciatic nerve. All other intermuscular connective tissue was left unaffected at the

level of the muscle bellies of TA and EDL. Only proximally and distally the connective tissue of the lower leg was further interfered with, in order to be able to free the proximal tendon of EDL and the distal tendon of the TA from their origin and insertion respectively. The freed tendons were attached to force transducers. Both EDL and TA were fully recruited and maximally active by supramaximal stimulation (100Hz) of the sciatic nerve at the level of the thigh. The tibial nerve branching from the sciatic nerve was cut, so in effect activity was limited to the whole peroneal nerve, innervation both TA and EDL (as well as the peroneus muscle group and extensor hallucis longus muscle).

During these experiments the length of EDL was kept constant at one of two states: (1) at a length of 32 mm, i.e., higher than its optimum length and (2) at a length of 27 mm, i.e., a length between its optimum and active slack lengths. As the length of EDL was kept constant, TA length was varied from low to high lengths in order to determine isometric length force characteristics.

b) Proximal as well as distal force measurements for EDL

In this case similar methods of exposing the proximal and distal tendons of EDL and TA respectively were used as described above. The connective tissue around the muscle bellies was left intact. However, in addition the four EDL distal tendons were exposed as well, and tied together at a reference length, to be attached to a force transducer. This means that for EDL, force is measured both at the proximal and distal end simultaneously. The distal tendons of TA and the extensor hallucis longus muscle (HAL) were tied to each other and attached to a third force transducer. Thus, these two muscles tendon complexes were mechanically coupled (TA+HAL) and activated simultaneously. They were kept at a low but constant length.

Results

a) Interaction of TA length change with EDL proximal force

Figure 8 (upper panel) shows an example of TA length force data as well as force data for EDL being maximally activated at low constant length. At lower TA lengths yielding notable TA forces (i.e., $Fm_{TA} > 0.5$ N) EDL force was relatively constant (as variations of measured EDL force were limited to less than 0.04 N). However, at very low TA lengths, yielding low levels of TA force that are hard to distinguish from zero, EDL force was increased. Therefore it is concluded that EDL force is a complex function of TA length. It should be noted however, that for the conditions imposed, the size of the effect is rather limited (to approximately 0.1 N, which is approximately 0.6 % of EDL optimum force).

With active EDL kept at constant high length (Fig. 8, lower panel), the force of EDL is dependent on length of the active TA: yielding increasing EDL forces at the lower half of the ascending limb of the TA length force curve for higher TA lengths and, after reaching an optimum, decreasing EDL forces with increased length of TA. The range of variation of EDL forces as function of TA length amounted in these conditions to 0.15 N, i.e., approximately 8.4% of this EDL muscle optimum force.

It is concluded that interaction, between properties of TA and EDL muscles, was found and that this interaction was a function of both EDL and TA lengths.

These preliminary results are in general compatible with the concept of myofascial force transmission out of the muscle by other than a tendinous path. However, it should be noted that they do not constitute unequivocal proof of *extramuscular* myofascial force transmission as it is conceivable that there could be some interaction between muscular properties (e.g., muscle length) without an actual transmission of force by an extramuscular path.

b) Simultaneous proximal and distal force measurement for EDL

A number of active muscle lengths, just below optimum length were obtained by moving the proximal EDL force transducer to the target length. Subsequently an isometric contraction at that length was performed, while EDL force was measured proximally and distally (Fig. 9). Note that proximally and distally measured EDL forces were not fully equal during build up of the force early in the tetanus. After building up force to tetanic levels, a steady decline of force in time, characteristic for tetanic contractions near optimum length, was seen for both proximal and distal transducers. Note however the permanent difference in force level for the two transducers during this phase (compare EDLprox1 and EDLdist1 traces in Fig. 9): EDL force at the distal force transducer was approximately 0.24 N or 3.6% lower than at the proximal transducer. This is a clear indication that additional to the tendinous path, a parallel pathway must exist for force to be transmitted from the muscle between its proximal and distal ends.

During the early force plateau, in a second contraction at slightly higher EDL lengths ($\Delta l = 1$mm), the force measured proximally, but not distally, increased

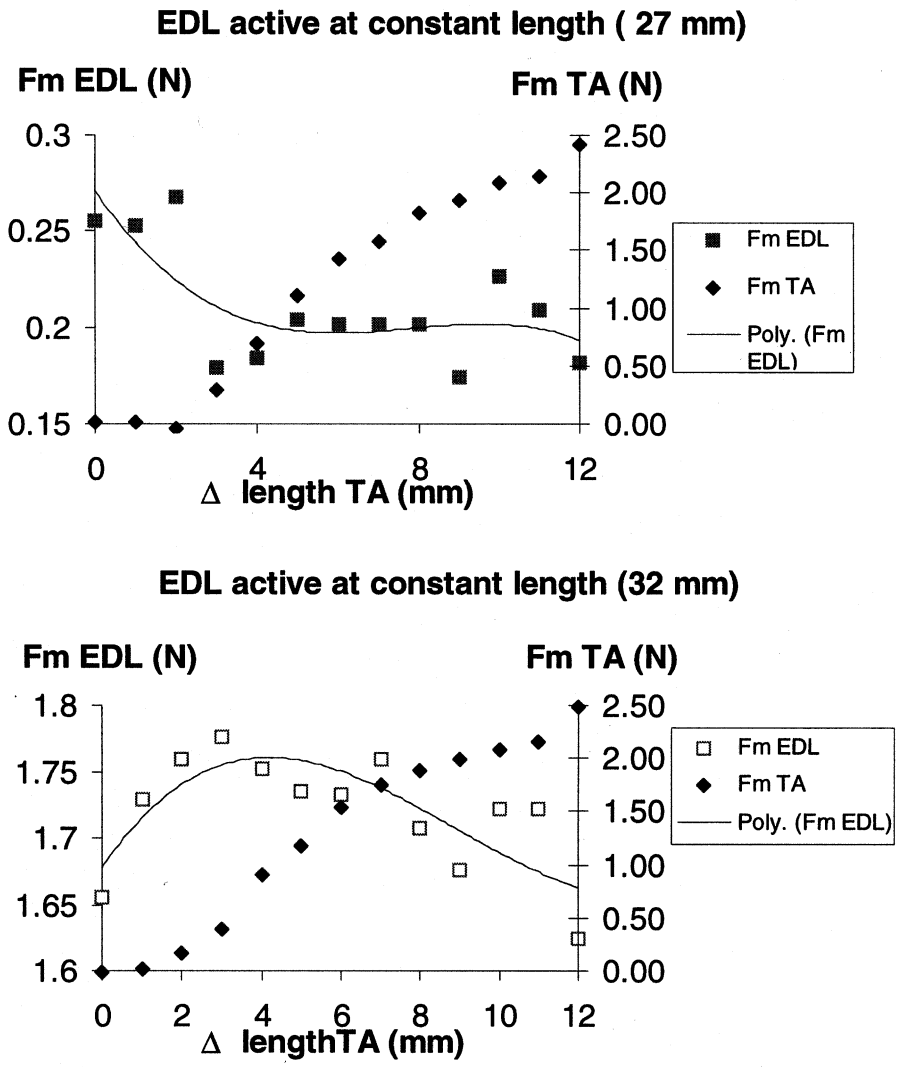

Fig. 8. Length force characteristics of a rat tibialis anterior muscle (TA) and total force (Fm) exerted by its adjacent extensor digitorum longus muscle (EDL), represented as function of TA length.
Top panel: For EDL activated a contant low length.
Lower Panel: For EDL activated at a constant high length.
For EDL force refer to the left axis (note particularity of scaling) and for TA force refer to right axis. Data is collected using simultaneous force measurement during isometric contractions at increasing lengths. The solid line represents a polynomial fitted trough EDL data points shows that EDL force is not independent of TA length.

a small amount compared to that of the previous length. During this contraction the connection to the proximal force transducer was severed suddenly (Fig. 9: trace EDLprox 2). Force exerted at the proximal transducer dropped rapidly to zero and remained at that level. Because of the disconnection force at the proximal transducer does no longer represent EDL force. Due to the release, a high velocity of shortening developed in EDL, and force at the distal transducer dropped temporary to near zero levels as well. After reaching zero force levels three phenomena are seen simultaneously: (1) Vibration occurring in the muscle did lead to instantaneous subzero forces; (2) Viscoelastic dampening caused substantial decrease of vibration amplitude on the force tracing in time; (3) A partially building up of force in time to a new and now constant isometric level. Note that after equilibrating, EDL force at the distal transducer did not return to zero values, but remained at low isometric levels (i.e., approximately 0.4 N) until the stimulation stopped.

These discrepancies in force between proximal and distal forces show unequivocally that force is transmit-

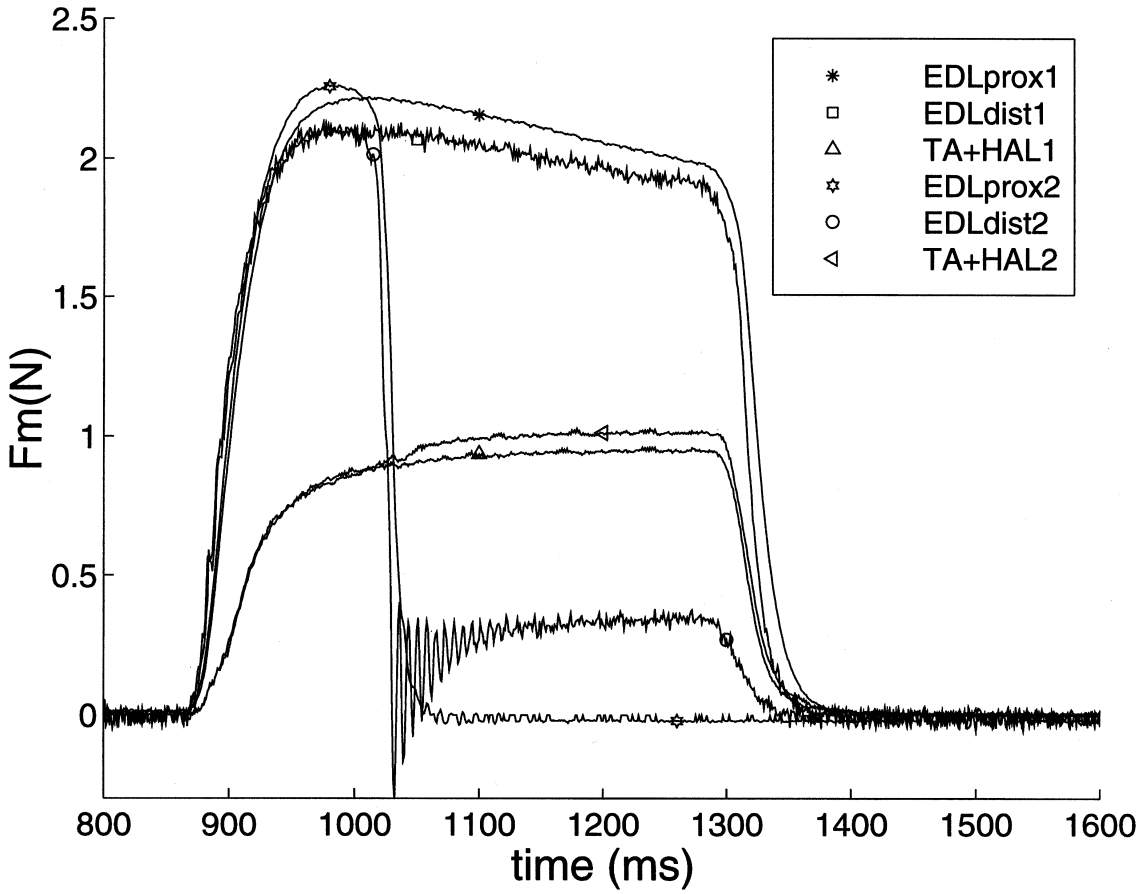

Fig. 9. Superimposed force time tracings during isometric contractions of rat extensor digorum longus muscle (EDL) and the complex of tibialis anterior muscle (TA) and hallucis longus muscle (HAL).
Tracings of total force (Fm) is shown as a function of time. The following tracings are superimposed (a) contractions with EDL at two lengths (indicated by suffix 1 or 2, length difference 1mm) both just below optimum length of EDL. (b) contractions of the complex of TA and HAL (TA+HAL1) and (TA+HAL2) while these muscles themselves were kept at a constant low length, yielding an approximate force level of 1 N. For EDL force was measured proximally as well as distally and for TA+HAL distally only. During the first contraction, conditions remained isometrically for all muscles (signals: EDLprox1, EDLdist1, TA+HAL1). During the second contraction, the connection of EDL to the proximal force transducer was suddenly released and therefore the signal of this transducer (EDLprox2) rapidly dropped to zero and did no longer represent EDL force after release. The effects of that release on signals from the other transducers (EDLdist2, TA+HAL2) was studied. Note that if no special force transmission would have occurred these signals would have been expected to either drop to zero levels (EDLdist2) or remain unaffected (TA+HAL2). Neither of these predictions were fulfilled: After transients EDLdist2 signals reached a steady force level of approximately 0.4 N after $t > 1150$ ms and the TA+HAL signal actually increased rapidly to higher levels of force.

ted from the EDL to other structures. The question must be raised to which structures the force is transmitted.

Figure 9 also shows raw data for TA+Hal forces. Note that the set length of these muscles was not changed, as is also evident from the near superposition of the two force traces (compare TA+HAL1 and TA+HAL2 traces) in the initial phase of the tetani. At a similar time to severing of the connection of EDL to the proximal force transducer, force exerted on the EDL+HAL transducer increased and equilibrated at higher levels. Two major alternatives for explanation for this increase in EDL+HAL force are: (1) either force exerted by EDL on the TA+HAL complex increased TA+HAL length somewhat, allowing an increase of force or (2) force transmitted previously from TA+HAL to EDL, after the proximal release of EDL could only be transmitted towards the TA or HAL distal force transducer probably by myo-tendinous transmission. However, analysis of images obtained during the tetanus at $t = 1080$ ms (i.e., well after the release of proximal EDL end for EDL2), show no detectable difference for lengths of TA+HAL in the two conditions. Such a length change is an absolute condition for hypothesis (1). Therefore the second explanation is preferred and would indicate the existence of *inter*muscular force transmission.

Its seems likely that force is transmitted from EDL to other structures than the TA+HAL complex as well to be able to keep EDL at such a length as to allow it deliver the force remaining at the distal transducer. At present we can not fully identify such structures, but an additional connective tissue connection to ground via the tibia or otherwise must be proposed (extramuscular force transmission).

GENERAL CONCLUSIONS

The above exploratory experimental results indicate *inter*- as well as *extra*-muscular force transmission in the dorsal flexor compartment of the rat leg. Therefore there is need for an in depth analysis of transmission of force out of EDL and other muscles. An analysis of connective tissue structures that could mediate transmission of force from muscle to other muscles or directly to bone is necessary as well. It is clear however that force transmission from muscle can not be considered a single system but should be regarded as a dual or even a multiple system.

Due to a focus on the destruction of muscle fibres in muscular dystrophies, interpretation of very exciting molecular and cell biological results regarding functions of sub- and trans-sarcolemmal molecules is generally phrased in terms of 'maintaining the integrity of muscle fibres'. In those sciences as well as in biomechanics, there is a need for a greater emphasis on identifying (supra-) molecular structures that actually can bear and transmit the force exerted by muscle fibres at their periphery and thus participate in myo-fascial force transmission.

The question needs to be addressed at all levels from experiments using whole limbs or isolated muscles as well as at the supramolecular level, which fraction of the muscle force is transmitted by which paths *in vivo* under specified conditions. It is clear that such work will require substantial efforts that will necessarily have to have a multidisciplinary character.

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